

Drivers of survival of translocated tortoises

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Abstract

Translocation of animals, especially for threatened and endangered species, is a currently popular but very challenging activity. We translocated 158 adult Agassiz's desert tortoises (*Gopherus agassizii*), a threatened species, from the National Training Center, Fort Irwin, in the central Mojave Desert in California, USA, to 4 plots as part of a long-distance, hard-release, mitigation-driven translocation to prevent deaths from planned military maneuvers. We monitored demographic and behavioral variables of tortoises fitted with radio-transmitters from 2008 to 2018. By the end of the project, 17.72% of tortoises were alive, 65.82% were dead, 15.19% were missing, and 1.27% were removed from the study because they returned to Fort Irwin. Mortality was high during the first 3 years: >50% of the released animals died, primarily from predation. Thereafter, mortality declined but remained high. After 10.5 years, survival was highest, 37.50% (15/40), on the plot closest to original home sites, whereas from 2.56% to 23.68% remained alive on the other 3 release plots. Surviving tortoises settled early, repeatedly using locations where they constructed burrows, compared with tortoises that died or disappeared. Models of behavioral and other variables indicated that numbers of repeatedly used locations (burrows) were a driver of survival throughout the study, although plot location, size and sex of tortoises, and distance traveled were contributors, especially during early years. Because >50% mortality occurred, we considered this translocation unsuccessful. The study area appeared to be an ecological sink with historical and current

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anthropogenic uses contributing to habitat degradation and a decline in both the resident and released tortoises. Our findings will benefit design and selection of future translocation areas.

KEYWORDS

dispersal, *Gopherus agassizii*, mitigation-driven translocation, Mojave Desert, mortality, movements, retention, settling

The International Union for Conservation of Nature (IUCN 2013:1) defined translocations as “the human-mediated movement of living organisms from one area, with release in another” for conservation. In contrast, mitigation-motivated or mitigation-driven translocations are strategies to mitigate or minimize effects of development by moving species to avoid harm (Dodd and Seigel 1991, Germano and Bishop 2008, Sullivan et al. 2014, Germano et al. 2015). Mitigation-motivated translocations are more common than those for conservation purposes, are frequently less well documented, and often lack scientific designs (Germano et al. 2015). Berger-Tal et al. (2020:121) noted that they “... are a high-cost endeavor with a history of failures.”

For >30 years, numerous authors discussed efficacy, ethics, and problems associated with translocations of chelonians and other reptiles (Berry 1986a, Burke 1991, Dodd and Seigel 1991, McCoy and Berry 2008, Sullivan et al. 2014). Authors expressed concerns about rationale and outcome for such projects, whether motivated by conservation or to offset negative effects of development. Developers and land managers often used mitigation-driven translocations to solve existing problems (Cozad et al. 2020, Scott et al. 2020) and to deal with human-wildlife conflicts (Bertolero et al. 2007, Attum et al. 2010). Views of measuring success differed among authors and species. Nevertheless, some agreement existed on defining success as the establishment or enhancement of a viable or self-sustaining population with evidence of new recruits (Dodd and Seigel 1991, Germano and Bishop 2008, Riedl et al. 2008). Measuring success was best accomplished by long-term monitoring or monitoring based on the time for the species to reach reproductive maturity or generation time, survival, retention of the translocated individuals at the chosen release site, and assimilation into the host population, if present (Berry 1986a, Burke 1991, Dodd and Seigel 1991). Funding for maintaining long-term monitoring of long-lived species was a major challenge (Burke 1991, Dodd and Seigel 1991, Germano et al. 2015, Berger-Tal et al. 2020). Authors emphasized the importance of science-based designs for translocation: knowledge of the biological constraints and behaviors of translocated and host populations, including disease and genetics, suitability of recipient sites, and reporting results (Berry 1986a, Dodd and Seigel 1991, Bauder et al. 2014, Germano et al. 2015).

The United States Fish and Wildlife Service (USFWS) listed Agassiz's desert tortoise (*Gopherus agassizii*; desert tortoise) as a federally threatened species in 1990, and the IUCN placed the species on the Red List of critically endangered species in 2021 (USFWS 1990, Berry et al. 2021). Desert tortoises, comparable to some other testudinids, share traits of longevity of >60 years, a lengthy period to achieve sexual maturity (17–20 yr), low fecundity, and a generation time estimated at 32 years (Woodbury and Hardy 1948, Hardy 1976, Turner et al. 1987, Medica et al. 2012, Berry and Murphy 2019). These traits present challenges for long-term monitoring of translocation projects to determine outcomes (Burke 1991, Dodd and Seigel 1991). Demographic analyses of desert tortoise populations indicated that males are larger than females, and sex ratios of adults were 1:1 in most relatively undisturbed populations 40 years ago (Berry and Murphy 2019). A minimum density of 3.86 adults/km² was considered necessary to maintain a viable population (USFWS 1994, 2011). For the desert tortoise, life in the desert is additionally challenging with extremes of temperatures, frequent droughts, and infrequent and unpredictable sources of food and water (Henen et al. 1998). Desert tortoises escape these extremes by spending >90% of their lives underground in burrows, rock shelters, and caves (Woodbury and Hardy 1948, Burge 1978, Nagy and Medica 1986, Mack et al. 2015). Many burrows are placed under large, shade-giving shrubs (Burge 1978). Desert tortoises tend to show fidelity to underground retreats and use areas (Woodbury and Hardy 1948, Burge 1978, Freilich et al.

2000, Drake et al. 2015). Resident adult tortoises have defined home ranges, which are larger for males than females, and males also move and travel more than females (Woodbury and Hardy 1948; Burge 1977; Harless et al. 2009, 2010). Tortoises know where water collects for drinking during rainfall (Medica et al. 1980) and avoid barren areas such as sites severely degraded by livestock or sites with users of recreation or other vehicles (Bury and Luckenbach 2002, Berry et al. 2013).

In 2001, the United States Congress passed the Fort Irwin Military Land Withdrawal Act of 2001 allowing for the expansion of the National Training Center (NTC) at Fort Irwin in the central Mojave Desert, California, USA (U.S. Congress 2001). The expansion affected several hundred desert tortoises in a critical habitat unit on the southern part of the NTC and created a need to prevent tortoises from being killed when military training and maneuvers with tanks and other armored vehicles occurred there. The USFWS authorized translocation of the tortoises as part of a research permit (USFWS TE-102235-0). Recent, long-distance translocations with the species provided indications of what might be expected (Field et al. 2003, 2007; Nussear et al. 2012). These studies used a mix of captive and previously translocated tortoises held for indeterminate periods of time at the Desert Tortoise Conservation Center in Nevada, USA. After translocation, the tortoises were monitored for periods of 1 to 3 years.

Our translocation was a mitigation-driven, hard release, long-distance project (≥ 500 m), compared with a soft release (tortoises kept in pens at translocation sites to acclimate prior to release), and a short-distance translocation (tortoises translocated within their probable use areas or < 500 m). Heaton et al. (2008) spent 3 years in pre-planning to select appropriate sites for release. The overarching goal of our project was to improve our understanding of behavioral factors affecting survival of wild, resident tortoises when translocated long distances outside their use areas. For our objectives, we predicted that locations of release plots would not affect survival because of careful pre-selection (Heaton et al. 2008), and that size and sex of tortoises were likely to affect survival because males are larger than females and potentially less vulnerable to predators (Berry and Murphy 2019). Males, however, travel more and have large use areas, potentially placing them at risk (Berry and Murphy 2019). We also predicted that tortoises with greater site fidelity to their new home sites or dispersed shorter distances (≤ 1.6 km) and settled sooner (i.e., repeatedly used locations during periods of temperature extremes) would be more likely to survive (Field et al. 2007, Nussear et al. 2012).

STUDY AREA

The study area was in the Superior-Cronese critical habitat unit for tortoises and covered an estimated 1,183 km² that included both the tortoise home sites on the NTC, Fort Irwin, and the translocation area where tortoises were released south of the NTC in the central Mojave Desert, San Bernardino County, California (Figure 1; USFWS 1994). We translocated tortoises 7.36–42.54 km from their home sites to designated release points on release plots. The southern boundary of the NTC formed the northern boundary of the translocation area, which extended south to an interstate highway (I-15). Several mountain ranges formed other boundaries, including the Calico Mountains in the west and southwest, and the Cronese Mountains to the east. Prior to the translocation, I-15 and Fort Irwin Road, the only paved road within the study area, received tortoise-exclusion fencing to prevent tortoises from entering these high-traffic roads. We selected the 4 release plots based on a spatially explicit, decision-support system developed by Heaton et al. (2008). Each release plot was approximately 2.58 km² and similar in perennial vegetation and general topography to the home sites. Resident tortoises were present on the plots and throughout the translocation area at densities of 6.2 adults/km² in 2004 (USFWS 2015).

The translocation area was fragmented by the Coyote Dry Lake playa, paved and dirt roads to the NTC, scattered residences, mines, and points of interest (Figure 1). Land uses included livestock grazing (in the past), mining, and, from the 1970s onward, vehicle-oriented recreational use on numerous dirt roads and trails, including cross-country races and tracks from unauthorized cross-country travel (Figure 1; Berry and Murphy 2019, U.S. Bureau of Land Management [USBLM] 2019). The historic Spanish Trail and the Manix Trail, a major military vehicle

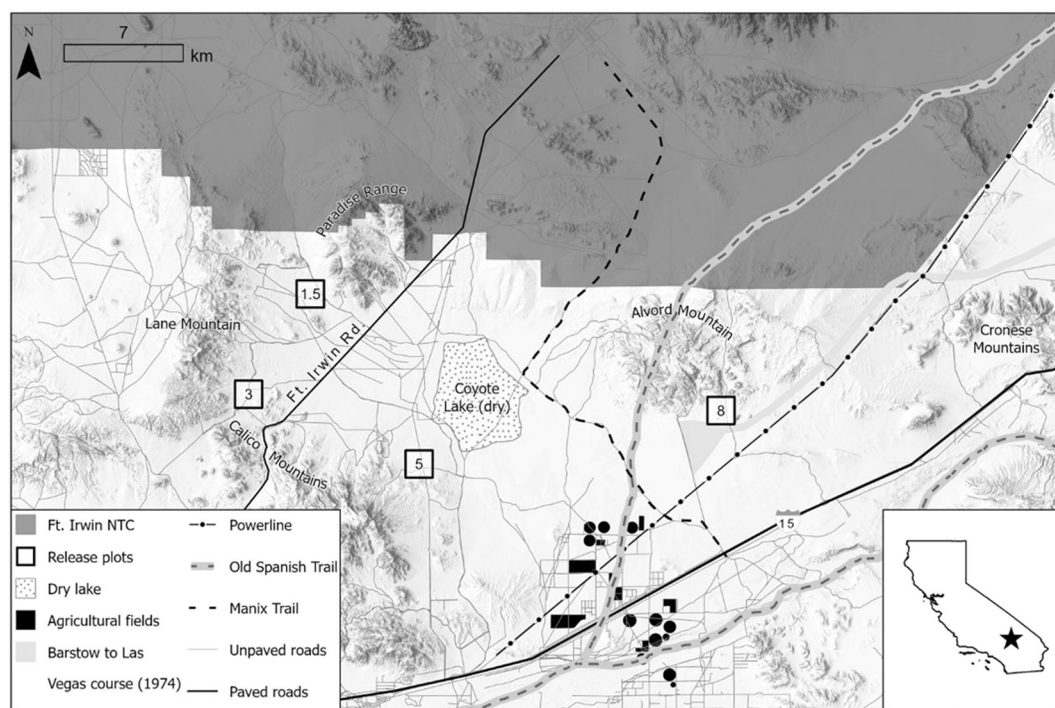


FIGURE 1 The study area for the translocation of adult Agassiz's desert tortoises in 2008, including the Fort Irwin National Training Center (Ft. Irwin NTC) and the translocation area to the south in the central Mojave Desert, California, USA. The figure shows locations of 4 release plots, topographic relief, and anthropogenic disturbances. Only major unpaved roads are shown as fine lines, not the numerous trails and roads created by vehicle-oriented, off-highway recreation.

and tank route, crossed the translocation area from the NTC to I-15 (Figure 1). Both trails have limited cover of shrubs because of use. The former start area for the Barstow-to-Las Vegas motorcycle race involving approximately 10,000 visitors and participants was in the central part of the translocation area, and the route led east to Las Vegas (USBLM 1974, 1975; Figure 1). The area was severely degraded from past vehicle use. Trash was common throughout and target shooting occurred in the vicinity of 3 plots.

Topography and vegetation varied from valleys, playas, alluvial fans, and low hills to rocky slopes. Elevations peaked at 1,280 m in the Calico Mountains and were lowest at Coyote Lake (dry, 540 m). A range of elevations occurred on the 4 plots: plot 1.5, \bar{x} = 710.9 m (range = 670.8–749.3 m); plot 3, \bar{x} = 801.3 m (range = 754.9–867.4 m); plot 5, \bar{x} = 609.7 m (range = 568.0–661.5 m); and plot 8, \bar{x} = 687.7 m (range = 658.7–745.9 m; Figure 1). Vegetation of perennial shrubs was one of several creosote bush (*Larrea tridentata*) and white bur-sage (*Ambrosia dumosa*) associations, often with cheesebush (*Ambrosia salsola*), desert tea (*Ephedra californica*), rayless goldenhead (*Acamptopappus sphaerocephalus*), box-thorn (*Lycium pallidum* var. *oligospermum*), Mojave-indigo bush (*Psoralea arborescens*), and Mojave aster (*Xylorhiza tortifolia*; <https://www.wildlife.ca.gov/Data/VegCAMP/Natural-Communities>, accessed 1 Oct 2022). In the southern part of the translocation area and in the vicinity of Coyote Lake and other playas, shrubs included allscale (*Atriplex polycarpa*) and other species of saltbush (*Atriplex* spp.).

The vertebrate fauna of the central Mojave Desert and our study area was composed of species typically found in creosote bush and saltbush plant communities (Rowlands et al. 1982). Predators of adult tortoises included coyotes (*Canis latrans*), American badgers (*Taxidea taxus*), bobcats (*Felis rufus*), domestic or feral dogs, golden eagles

(*Aquila chrysaetos*), and common ravens (*Corvus corax*). Common ravens are subsidized predators and are threats to all sizes of tortoises in the translocation area (Boarman and Berry 1995, Kristan and Boarman 2003, Andrew Walde, Walde, Research and Environmental Consulting, unpublished report).

The central Mojave Desert has 4 distinct seasons: spring (late Mar to mid-Jun), summer (mid to late Jun through the third week of Sep), fall (late Sep through the third week of Dec), and winter (late Dec through the third week of Mar; Rowlands 1995). The average annual temperature was 17.7°C, mean January minimum was 0.4°C, and mean July maximum was 39.1°C. Temperature extremes frequently exceeded 45°C in late spring and summer; on average below freezing temperatures occurred on 57 days between late October and March (Rowlands 1995). Precipitation was typical of the central Mojave Desert. Long-term, 20-year annual averages for rainfall during the hydrological year (1 Oct–30 Sep) and fall-winter averages (1 Oct–31 Mar) prior to 2008 were 108.8 mm and 84.2 mm, respectively, based on grouped averages for each of the 4 release plots (800-m and 4-km datasets, PRISM Climate Group, <http://prism.oregonstate.edu>, accessed 20 Aug 2020). Most precipitation (77.3%) occurred from October through March (fall-winter rainfall), producing annual and herbaceous perennial plants, among which tortoises selected favored forage species low in potassium (Oftedal 2002, Oftedal et al. 2002, Jennings and Berry 2015).

METHODS

Translocating and tracking tortoises

Three years prior to translocation (2005–2007), research teams fitted several hundred tortoises on the NTC with radio-transmitters (RI-2B, 14 g; Holohil, Carp, Ontario, Canada) and conducted periodic health examinations using established protocols (Berry et al. 2015). Briefly, we examined each tortoise for posture, behavior, and clinical signs of upper respiratory tract disease caused by *Mycoplasma agassizii* and *M. testudineum* (Jacobson et al. 2014) and oral lesions (Christopher et al. 2003, Jacobson et al. 2012). We drew blood samples for enzyme-linked immunoassays (ELISA) to test for antibodies for pathogens that cause and transmit upper respiratory tract disease (Jacobson et al. 2014, Berry et al. 2015). We selected 158 healthy adult tortoises from the several hundred tortoises available for translocation. Tortoises were adults ≥ 180 mm in carapace length at the midline (MCL) and were in 3 size classes: small or generally young adults, 180–208 mm; adults, 209–239 mm; and large adults, ≥ 240 mm. Initially scheduled for 2007, we postponed the translocation because of drought. With sufficient rain in winter of 2007–2008 to break the drought and increase forage available for tortoises in early spring of 2008, we initiated translocation.

From 26 March through 8 April 2008, we collected tortoises from their home sites on the NTC and transported them on the same day in individual, disinfected totes to the 4 release plots. During collection, transport, and release, we kept tortoises in the shade within air temperature limitations ($\leq 35^\circ\text{C}$). We distributed tortoises 200 m apart on each release plot, alternating between male and female, releasing 38 to 41 tortoises per plot in approximately even sex ratios (Table 1). The field team placed each tortoise under the closest shrub to its assigned location, recorded data on the release point (e.g., time, locations in the Universal Transverse Mercator system, shrub species), and initial behaviors after the tortoise was released, such as resting in the shade, basking in the sun, walking, sniffing the ground, and foraging. Over the 10.5-year study, we tracked the tortoises using 3 types of receivers (R2000, Advanced Telemetry Systems, Isanti, MN, USA; Garmin GPSMap 62s, Garmin, Olanthe, KS, USA; and R-1000, Communications Specialists, Orange, CA, USA) and Telonics antennas (3-FB antennas, Telonics, Mesa, AZ, USA).

During the first week after release (26 Mar–14 Apr), we tracked and located tortoises daily. At each visit, we collected data on specific and general locations, behavioral observations, and general condition of the tortoise. Thereafter we recorded data on locations at the following intervals, unless behavioral or health dictated more frequent checks: every 2 to 3 days during the second to sixth week after release; every 4 days from the seventh week after release until the end of May; once per week between 1–20 June; and once per month beginning in July. Monthly monitoring continued through October 2018. When we found tortoises dead, we recorded data on location (Universal

TABLE 1 Sample sizes, sexes, and midline carapace lengths for 158 adult Agassiz's desert tortoises translocated from Fort Irwin National Training Center, California, USA, in spring 2008 to 4 experimental release plots.

Plot	n	Sex	Carapace length at the midline (mm)		
			\bar{x}	SD	Range
1.5	19	Female	225.4	12.1	201–245
	19	Male	260.8	26.0	191–287
3	22	Female	226.9	16.8	180–254
	19	Male	246.3	32.5	153–276
5	19	Female	235.2	18.3	211–280
	20	Male	256.0	30.8	188–285
8	20	Female	223.7	13.8	197–245
	20	Male	253.9	24.1	193–289

Transverse Mercator system); noted whether the remains were under a shrub, in the open, or in a wash; the position (right side up, upside down); amount of remains (entire tortoise, shell only, fragments); and evidence of cause or potential causes of death based on forensic evidence, location, and condition of remains (Berry 1986b, Berry et al. 2006). For example, tracks, scat, marks on the ground from a predator—associated with puncture wounds, chewing, gnawing, and breaks in the shell-skeletal remains—provided evidence for the species of carnivorous predator. If the tortoise was killed rather than scavenged after death, pieces of shell were twisted and distorted by torsion, because the shell is more pliable prior to and during death when a carnivore is tearing at the shell (Berry et al. 2006). We categorized a tortoise crushed on or adjacent to a dirt or paved road or in vehicle tracks as a vehicle kill. Evidence of predation by a common raven included peck marks and a hole or holes in the anal and inguinal area, gutted, and occasionally with the eyes and head pecked (A. P. Woodman, Kiva Biological Consulting, personal observations; A. D. Walde, Walde Research and Environmental Consulting, unpublished report). A kill by a golden eagle was typically associated with a perch, nest, or a steep and rocky area, with breaks in the shell typical of being dropped from a height and without the chewing and gnaw marks typically made by a mammalian predator (K. H. Berry, U.S. Geological Survey, unpublished report). Tortoises dying of hyperthermia when body temperatures reach 39.5°C produce copious saliva, which flows down the neck and onto the gular horn; death occurs when body temperatures reach 43.0°C (Brattstrom 1961, McGinnis and Voigt 1971). Dried saliva on the head and neck of recently dead tortoises in upright positions with no evidence of scavenging indicated hyperthermia. If the death was caused by a mammalian carnivore but the species could not be determined, we treated it as a mammalian carnivore. If dogs or coyotes were involved but it was not clear which was responsible, we assigned the death to canid. We treated some deaths as undetermined. Before collecting the remains, we took a series of digital photographs of the remains and vicinity, including evidence of predators, scavengers, vehicles, and human activities. We then collected remains for later evaluation at the United States Geological Survey laboratory in Riverside, California, and Reno, Nevada.

Data analysis

Death rates

We evaluated the status of tortoises (live, missing, dead), and the probable causes of death for those found dead, by sex, size, and release plot. We calculated annual and annualized death rates (multiple years or partial years)

beginning in spring 2008. For simplified death rates (1 yr), we used the equation D/n where D = the number of dead tortoises with transmitters found in a specific year, and n = the number of live tortoises with transmitters at the beginning of the specific year. For annualized death rates, we used the equation $(1 - [1 - D/n]^{1/t}) \times 100\%$, where D = number of dead tortoises with transmitters in a given period, n = the number of known live and dead tortoises with transmitters in a given year, and t is the number of years or parts of years in a given survey period. Annual or annualized survival was the reciprocal of the annual or annualized mortality rate.

Distance traveled, dispersal, settling behavior, and use areas

The receivers and global positioning system equipment used for tracking provided tortoise locations within a few meters. We used these locations to calculate metrics of distance traveled, settling behavior, and use areas. We conducted all calculations and statistical analyses in R (version 4.1.0; R Core Team 2021) and ArcGIS Pro (Esri, Redlands, CA, USA).

For each tortoise, we calculated the minimum distance traveled between subsequent observations as a straight-line distance. We then used these straight-line distances to calculate 2 metrics of distance traveled: distance traveled over the 10.5 years (or life of the tortoise) as the sum of the distances traveled between each observation, and mean distance that a tortoise traveled per observation as the average of the distances traveled between observations. We also calculated the distance each tortoise was translocated from home site on the NTC to release location on a release plot as a straight-line distance between these 2 points.

We examined settling behavior by quantifying dispersal, retention on release plot, and repeated use of a location (burrow, den, cave). We defined dispersal as the farthest point from release location and considered 2 points: dispersal within the first year of the study and dispersal over 10.5 years (or life of the tortoise). We limited our calculations of dispersals to tortoises that survived past 14 days. We compared number of observations, metrics of distance traveled, and dispersal distances among plots and between sexes. We tested for an interaction effect between the 2 variables with a 2-way analysis of variance (ANOVA). Following a significant 2-way ANOVA, we conducted Tukey's *post hoc* multiple comparisons.

To estimate retention on release plots, we established individual boundaries for each tortoise by overlaying each release location with a buffer with a radius of 1.6 km, which was equivalent to the width of each release plot. We determined if any tortoises remained within their buffer area or their plot boundary for 10.5 years (or life of the tortoise). For those that moved outside of their plot boundaries, we estimated the time it took and if the tortoise returned or remained outside of the boundary. We made comparisons among release plots.

We quantified the number of repeatedly used locations (i.e., repeat locations) during periods of temperature extremes (i.e., winter and summer; Woodbury and Hardy 1948, Mack et al. 2015). We defined a repeat location as one that was used among seasons. For example, we did not consider repeated use of a location during a single season within a year to be a repeat location. First, we combined locations within a 6-m radius using the intersect tool (ArcGIS Pro 2.8) to compensate for the error range of global positioning system units and dissolved them together with the dissolve tool (ArcGIS Pro 2.8), to establish a unique identity for each location. We then joined the intersected and dissolved points together with a one-to-many spatial join (ArcGIS Pro 2.8) and computed the number of repeat locations for each tortoise. We compared the number of repeat locations among release plots and between sexes with a zero-inflated Poisson (ZIP) model (zeroinfl function in package pscl; Jackman 2020). The ZIP model enabled examination of the effects of explanatory variables on the count response (i.e., number of repeat burrows) and the probability of a zero count (Wenger and Freeman 2008).

For tortoises with repeat locations, we quantified the time to first repeat location and compared among release plots, sexes, and status (alive, dead, missing). We tested for an interaction effect between the 3 variables with a 3-way ANOVA. We also evaluated repeat locations established in summer 2008 (i.e., during the first period of

extreme temperatures) to determine how much time elapsed for a tortoise to repeat ≥ 1 of these locations and how many times these 2008 locations were used during different periods of extreme temperatures.

We estimated use areas using home ranges and settlement areas. We used traditional methods to estimate 2 sizes of home ranges. To represent the full home range, we fitted a minimum convex polygon (MCP), which draws the smallest polygon around all locations using exterior points (`mcp` function in package `adehabitatHR`; Calenge 2006). To calculate an area from the MCP, we removed tortoises without 3 unique locations from the analysis. To represent the core use area of the home range, we used kernel density estimation for calculating the area associated with a 50% probability of finding the tortoise (`getverticeshr` function in package `adehabitatHR`; Calenge 2006). We used the reference smoothing parameter (h^{ref}) for kernel density estimation calculations and removed tortoises with < 30 locations (Seaman et al. 1999). Row and Blouin-Demers (2006) recommended traditional methods like MCP and kernel density estimation for studies of herpetofauna, even though they may include areas of unusable habitat, or underestimate areas of habitat use (Fleming et al. 2015, Averill-Murray et al. 2020).

In addition to home ranges, we calculated a settlement area for each tortoise by circumscribing all observed locations and calculating the radius of the resulting buffer. We compared sizes of home ranges and settlement areas between plots and sexes. We tested for an interaction effect between the 2 variables with a 2-way ANOVA. We log-transformed home ranges and settlement areas to meet the assumptions of normality and constant variance. Following a significant 2-way ANOVA, we conducted Tukey's *post hoc* multiple comparisons.

Models of survival of the translocated population

We used generalized linear models with a logit link for binary outcomes to identify explanatory variables predicting survival and how these predictors changed over time. We ran 11 generalized linear models with subsets of data for each year following the release (2008). For these analyses, we removed missing tortoises. We removed an additional 5 tortoises from the overall study: 3 were moribund, salvaged for necropsy, and treated as dead in the analyses of the year they were salvaged or when they died. We removed transmitters from 2 other tortoises because they returned to the NTC where additional tracking was not allowed. We treated these 2 tortoises as live in the analyses until we removed their transmitters in 2011; after 2011, we treated them as missing and did not include them in subsequent analyses.

To identify appropriate variables for developing a predictive model of survival, we examined 11 potential variables: release plot, sex, size of tortoise, total distance traveled, distance traveled per observation, distance between home site on the NTC and release site on the release plot, dispersal distance, size of home range, size of core use area, size of settlement area, and number of repeat locations. We conducted a Pearson correlation analysis with 9 continuous variables to identify variables correlated with one another. To reduce collinearity, we removed redundant information and simplified model structure without reducing the quality of prediction (Dormann et al. 2013). We removed total distance traveled and dispersal distance from the analyses because of correlation with mean distance traveled per observation. We also removed size of home range, core use area, and settlement area because these variables were correlated with one another and with mean distance traveled per observation. Therefore, the final set of models considered 5 variables, except for 2008, which did not include number of repeat locations because, with our definition, the first opportunity of a repeat location would occur in 2009.

Using 5 explanatory variables, we created a set of main effects models ($n = 32$) with all possible combinations of variables. The 2008 model set contained 4 explanatory variables and 16 possible models. We based model fit on second order Akaike's Information Criterion (AIC_c ; corrected for sample size) and identified the best fit model as the model with the lowest AIC_c . We then compared each model to the best fit model and ranked the models based on the difference between AIC_c values (ΔAIC_c). We reported models with ΔAIC_c values < 2 units along with the best fit model (Burnham and Anderson 2002). We calculated additional metrics of model fit including Akaike weights and evidence ratios. For each explanatory variable, we calculated relative variable importance and model-averaged

coefficients. We derived relative importance from the sum of weights of all models in which the specific variable occurred. We calculated model-averaged coefficients by averaging coefficient estimates for each variable over the models in which they occurred. We used the package *ModelInference* (version 1.70, <https://www.usgs.gov/staff-profiles/mark-herzog>, accessed Jul 2021). We further described a relationship between survival and number of repeat locations by fitting a logistic regression model to the data, which estimated the likelihood of survival based on the number of repeat locations. We highlighted the number of repeat locations that corresponded to a 50% level of survival.

RESULTS

Mortality and survival of translocated tortoises

Mortality was high during the project (Table 2) and began during the first few days. By the end of 3 months, 17.72% (28/158) of tortoises were dead and by the end of the first year, annualized death rates based on the partial year were 39.04% with values differing by plot (49/158 total; range = 16.31–61.60%; Table 3, Figure 2). The numbers of deaths continued to increase in the second year, and more than half were dead at the end of the third year. We predicted erroneously that location of release plots would not affect survival. Plot location was important, along with other factors, early in the translocation. For 2008 and 2009 combined, annualized mortality for all plots combined was 31.25% (range = 13.55–49.01%), with plots 3 and 5 having >3 times the rates of plot 8. Mortality declined between the third and final year of the project. Only 3 of 41 tortoises remained alive on plot 3 and 1 of 39 on plot 5 by the end of the study period (Figures 2 and 3). Death rates were likely higher than described because some missing tortoises were probably dead. Deaths were more likely to occur when tortoises were above ground and active; most deaths occurred in spring ($n = 47$), followed by summer ($n = 28$), fall ($n = 23$), and winter ($n = 6$).

The evidence indicated that mammalian carnivores killed 78.85% (82/104) of the dead tortoises. Among these deaths, coyotes killed 59.76% (49/82); the sources of the remaining kills (40.24%, 33/82) were treated generically as mammalian carnivores (coyotes, domestic dogs, American badgers, and bobcats). Deaths from mammalian predators were highest at plot 5, followed in descending order by plots 1.5 and 3 with plot 8 having the least.

Other sources of mortality included avian predation; common ravens killed 9 of 104, and a golden eagle killed 1 of 104. Two tortoises appeared to die of hyperthermia and a third from dehydration (2.88%, 3/104). Two tortoises were found dying and salvaged for necropsy, and a third salvaged tortoise was mortally wounded by a coyote (2.88%, 3/104). One tortoise died from a vehicle hit on a dirt road and another from envenomation from a rattlesnake, probably a speckled (*Crotalus mitchellii pyrrhus*) or Panamint rattlesnake (*C. stephensi*) based on necropsy (Berry et al. 2016). Causes for 4 deaths (4/104) were undetermined.

TABLE 2 Status of 158 adult Agassiz's desert tortoises translocated from the Fort Irwin National Training Center, central Mojave Desert, California, USA, in 2008 after 10.5 years. We considered 2 tortoises salvaged for necropsy and 1 tortoise removed after severe predator injuries to be dead. In addition, we removed 2 tortoises that returned to the National Training Center in September 2011 from the project.

Status	Total		Females		Males	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Alive	28	17.72	11	39.29	17	60.71
Missing	24	15.19	9		15	
Dead	104	65.82	61	58.65	43	41.35
Removed	2	1.27	0		2	
Total	158	100.00	81	51.27	77	48.73

TABLE 3 Mortality rates (simplified death rates for 1-yr periods or annualized mortality for <1-yr and >1-yr periods) and survival rates during the 10.5-year project, spring 2008 through fall 2018, for 158 Agassiz's desert tortoises translocated from the National Training Center, Fort Irwin, to 4 plots in the central Mojave Desert, California, USA. D = number of tortoises dead and *n* = starting number of known live tortoises for the period. Numbers of live tortoises were too low to calculate mortality and survival rates for plots 3 and 5 by the end of 2008, and for plots 1.5 and 8 by the end of 2010 and 2013, respectively.

Plot(s)	Period	D	<i>n</i>	Number of years	Mortality rate (%)	Survival rate (%)
All plots	2008	49	158	0.75	39.04	60.96
	2008–2018	104	158	10.5	9.72	90.28
Plot 1.5	2008	6	38	0.75	20.48	79.52
	2009	7	32	1	21.87	78.13
	2008–2009	13	38	1.75	21.28	78.72
Plot 3	2010	4	25	1	16.00	84.00
	2008	21	41	0.75	61.60	38.40
	2008–2009	27	41	1.75	45.88	54.12
Plot 5	2008	16	39	0.75	53.39	46.61
	2008–2009	26	39	1.75	46.62	53.38
Plot 8	2008	5	40	0.75	16.31	83.69
	2009	4	35	1.0	11.40	88.60
	2008–2009	9	40	1.75	13.55	86.45
	2010	1	31	1	3.23	96.77
	2011	1	28	1	3.57	96.43
	2012	0	25	1	0	100.00
	2013	2	25	1	8.00	92.00

By the end of the study when we removed transmitters and recorded final locations, 28 (17.72%) tortoises were alive (all plots combined), 104 (65.82%) were dead, 24 (15.19%) were missing with unknown status, and 2 (1.27%) had returned to the NTC (Table 2; Figures 1 and 3). As we predicted, more males (17) survived than females (11) for all plots ($\chi^2 = 1.29$, $P = 0.257$). Male to female ratios were 7:2 on plot 1.5, 1:2 on plot 3, 1:0 on plot 5, and 8:7 on plot 8. More tortoises released on plots 8 (37.5%, 15/40) and 1.5 (23.68%, 9/38) were alive than on plot 3 (7.32%, 3/41) and plot 5 (2.56%, 1/39; Figures 2 and 3). For plots 3 and 5, no additional deaths occurred after 2013 and 2014, respectively. We predicted that larger tortoises would be more likely to survive than smaller tortoises. All surviving males were in the large adult class and were ≥ 244 mm in MCL. Annualized survival for all plots combined was low at the end of the first year (0.75 yr), 60.96%, and remained low in the second year (Table 3). For the first 1.75 years combined, survival ranged from 53.38% to 86.45%, depending on the plot. Sufficient samples ($n \geq 25$) were available to estimate annual survival rates for plot 1.5 through 2010 and through 2013 for plot 8 (Table 3).

Distance traveled, movements, dispersal, and repeat locations

The mean (\pm SD) distance from home sites on the NTC to release locations on plots was 23.05 ± 10.22 km (range = 7.36–42.54 km) and differed by release plot (2-way ANOVA; $F_{3,150} = 45.815$, $P < 0.001$; Table 4). Tortoises

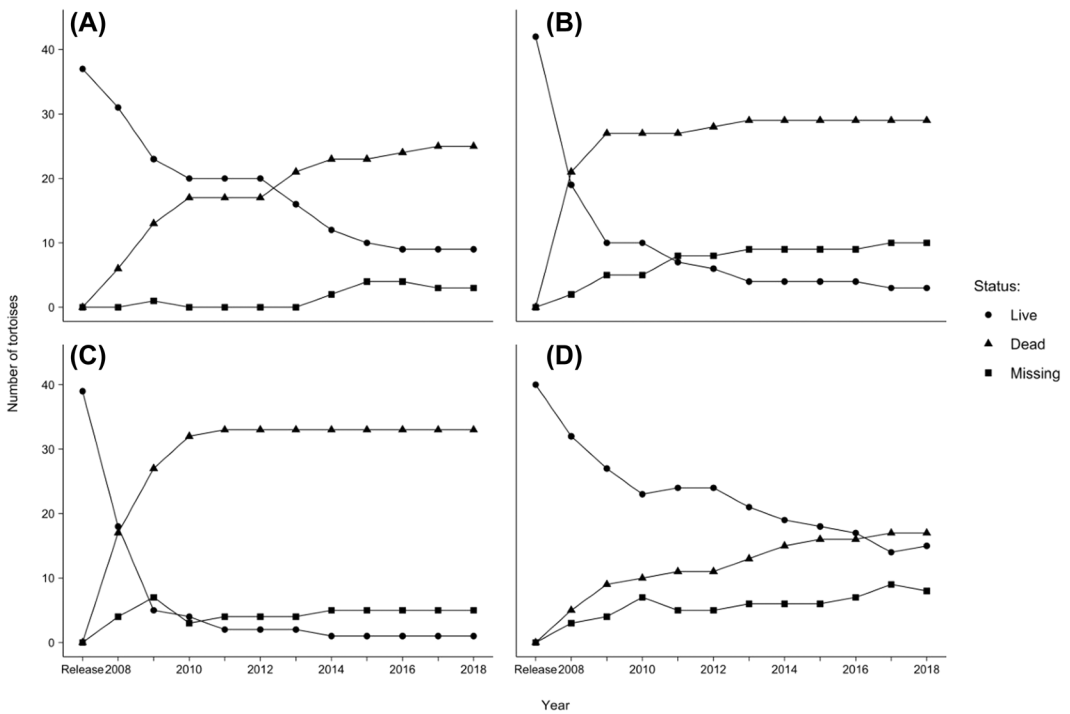


FIGURE 2 Changes in status of 158 live, dead, and missing adult Agassiz's desert tortoises translocated in spring 2008 from the National Training Center, Fort Irwin, California, USA, to 4 release plots (plot 1.5 [A], plot 3 [B], plot 5 [C], and plot 8 [D]) in the central Mojave Desert and tracked until fall 2018.

released on plot 8 were closer to their home sites compared to all other plots (Tukey's *post hoc*, $P < 0.001$), whereas tortoises released on plot 3 were the most distant compared to tortoises on plots 1.5 and 5 (Tukey's *post hoc*, $P < 0.001$). On average, we recorded 61 locations for each tortoise; however, the range was substantial, from one location for a tortoise killed by a coyote immediately after release, to approximately 150 locations for tortoises surviving 10.5 years. The number of locations varied among plots (2-way ANOVA; $F_{3,150} = 14.035$, $P < 0.001$). Tortoises released on plots 1.5 and 8 survived longer and subsequently had more locations than tortoises released on plots 3 and 5 (Tukey's *post hoc*, $P = 0.004$).

Distances tortoises traveled differed by release plot and sex (Table 4). Total distance traveled and distance traveled between observations varied among plots (2-way ANOVA, total distance: $F_{3,150} = 6.428$, $P < 0.001$; between observations: $F_{3,150} = 4.2$, $P = 0.007$). Tortoises released on plot 1.5 traveled longer total distances compared to plots 3 and 5 (Tukey's *post hoc*, $P = 0.015$), and those released on plot 8 traveled longer total distances compared to plot 3 (Tukey's *post hoc*, $P = 0.012$). This relationship was likely a result of longer survival; although tortoises released on plot 8 traveled longer total distances, they traveled shorter distances between observations compared to tortoises on plots 3 and 5 (Tukey's *post hoc*, $P = 0.015$). As we predicted, distances traveled also varied by sex (2-way ANOVA, total distance: $F_{1,150} = 36.534$, $P < 0.001$; between observations: $F_{1,150} = 22.578$, $P < 0.001$). As we expected, males traveled longer total distances (Tukey's *post hoc*, $P < 0.001$) and distances between observations (Tukey's *post hoc*, $P < 0.001$).

Dispersal in the first year differed by release plot and sex (2-way ANOVA, plot: $F_{3,141} = 4.227$, $P = 0.007$; sex: $F_{1,141} = 22.445$, $P < 0.001$; Table 4). Tortoises released on plot 8 dispersed shorter distances compared to plot 3 (Tukey's *post hoc*, $P = 0.011$) and plot 5 (Tukey's *post hoc*, $P = 0.045$). As we predicted, females dispersed shorter

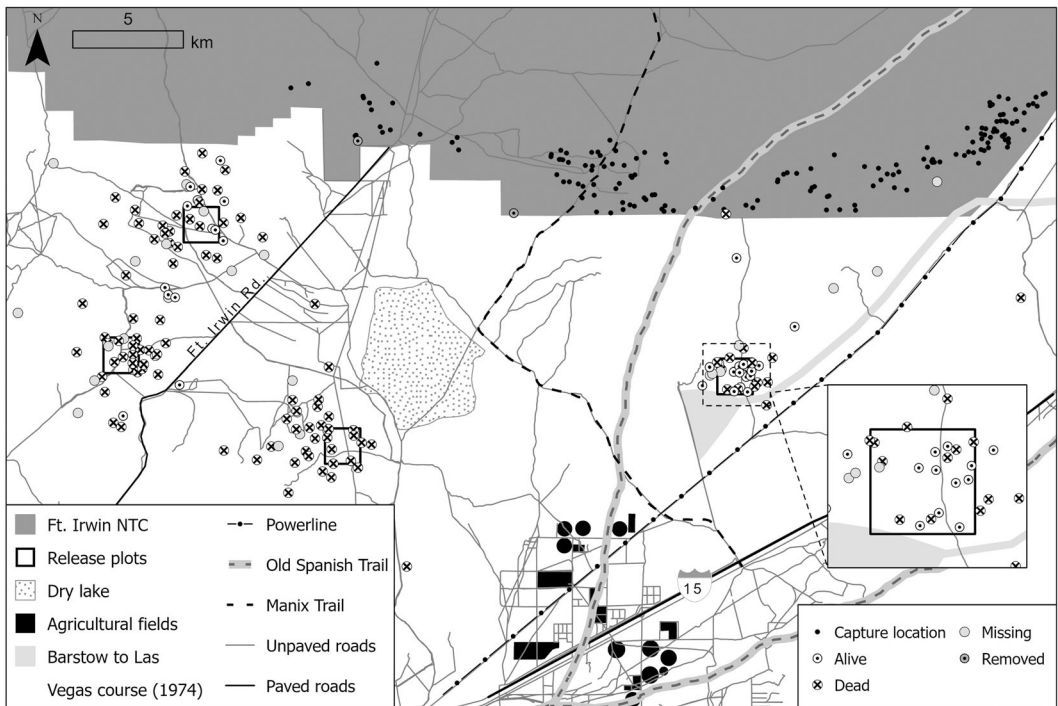


FIGURE 3 The original home site, final location, and status (live, dead, missing, removed) of 158 adult Agassiz's desert tortoises translocated from the Fort Irwin National Training Center (Ft. Irwin NTC) to 4 release plots in the central Mojave Desert, California, USA. The translocation occurred in early spring 2008 and ended in October 2018. Original capture sites on the National Training Center are shown as solid dots.

distances compared to males (Tukey's *post hoc*, $P < 0.001$). Dispersal after the first year, until the end of the study, continued to differ by sex but not plot (2-way ANOVA, plot: $F_{3,141} = 1.089$, $P = 0.356$; sex: $F_{1,141} = 28.748$, $P < 0.001$; Table 4), where females dispersed shorter distances compared to males (Tukey's *post hoc*, $P < 0.001$). By the end of the project, 20 of 158 tortoises dispersed >5 km. Two tortoises, both males from plots 8 and 3, traveled 12.57 km and 14.92 km to inside NTC boundaries by September 2011. Two additional tortoises from plot 8, 1 male and 1 female (found dead Oct 2013), dispersed 13.24 km and 13.77 km, respectively, whereas another female tortoise on plot 8 that survived the entire 10.5-year study, dispersed only 1.04 km. Twenty-four tortoises went missing, either moving beyond tracking range or experiencing transmitter failure, likely including damage by predators. More than half the missing tortoises were lost in the first 3 years (14/24) mostly on plots 3 and 5, where 7 and 4 tortoises went missing, respectively.

Counts and numbers of repeat locations differed by release plots (Table 4) and for the ZIP models (Table 5). Compared to tortoises on plot 8, tortoises on plots 3 and 5 were more likely to have no repeat locations and fewer numbers of repeat locations (44.57% and 75.34%, respectively). When we compared time to first repeat location among release plots, between sexes, and status (alive, dead, missing), we found no interaction but an effect of sex (3-way ANOVA, $F_{1,51} = 5.154$, $P = 0.028$). Females established a repeat location sooner than males (Figure 4).

Forty-three tortoises repeated a location they used in summer of 2008 in a later period of temperature extremes. Five tortoises repeatedly used multiple locations; 2 tortoises were located on plot 1.5 and 3 were on plot 8. Two additional tortoises, 1 each on plots 1.5 and 8, repeated a location established during the first summer in 10 different periods of temperature extremes. On average, these locations were repeated within 490.4 ± 578.6 days

TABLE 4 Summary of metrics of movement and settling behaviors by release plot and sex of 158 Agassiz's desert tortoises translocated from the Fort Irwin National Training Center (NTC), California, USA, spring 2008 through fall of 2018. Metrics included release distance = distance from home site on the NTC to release location on a release plot; total distance = total distance moved over the lifetime of the tortoise; between observations = average distance moved between observations; number of repeat locations; and dispersal as the farthest distance located from release location during year 1 and over the lifetime of the study or lifetime of the tortoise.

Plot	Sex	Release distance (km)			Total distance (km)			Between observations (km)			Number of repeat locations			Dispersal year 1 (km)			Dispersal lifetime (km)		
		\bar{x}	SD	Range	\bar{x}	SD	Range	\bar{x}	SD	Range	\bar{x}	SD	Range	\bar{x}	SD	Range	\bar{x}	SD	Range
1.5	Female	26.3	8.7	9.6-36.1	11.4	5.6	3.8-20.9	0.2	0.2	0.09-0.8	2.3	2.8	0-8	2.0	1.7	0.4-7.3	2.3	1.5	0.9-7.3
	Male	23.5	9.1	9.6-40.3	21.5	7.9	8.3-31.3	0.3	0.1	0.1-0.6	4.5	3.8	0-12	2.8	1.6	1.0-7.3	3.0	1.6	1.0-7.7
3	Female	30.8	9.5	15.6-42.5	8.0	7.0	0.1-29.8	0.3	0.2	0.03-0.6	0.7	1.7	0-6	2.5	1.8	0.4-6.5	2.7	1.8	0.4-6.5
	Male	32.6	9.5	13.9-42.0	13.8	9.9	0.01-31.5	0.4	0.2	0.002-0.9	0.8	1.9	0-8	3.3	2.2	1.1-8.6	4.1	3.3	1.1-14.9
5	Female	22.6	7.8	14.1-35.8	7.3	3.4	3.3-14.8	0.2	0.1	0.1-0.6	0.05	0.2	0-1	1.9	1.1	0.5-4.5	2.1	1.5	0.5-6.4
	Male	22.5	7.3	14.3-35.9	13.6	9.5	3.4-43.0	0.3	0.2	0.1-0.9	0.4	0.9	0-3	3.1	1.9	0.8-7.7	3.7	2.2	1.0-7.8
8	Female	12.8	3.5	7.8-17.6	11.2	9.1	0.3-32.8	0.1	0.1	0.05-0.5	4.3	3.5	0-9	1.3	1.0	0.4-4.7	1.9	2.9	0.4-13.8
	Male	13.2	4.4	7.4-21.3	21.2	10.1	2.9-38.3	0.3	0.1	0.1-0.6	3.8	3.4	0-11	2.6	1.8	0.4-8.0	4.6	3.7	1.1-13.2

TABLE 5 Estimated coefficients of the zero-inflated Poisson model for the number of repeat locations (burrows) used by adult Agassiz's desert tortoises translocated from Fort Irwin National Training Center, in the central Mojave Desert, California, USA, to 4 release plots, spring 2008 through fall 2018. Predictor variables included release plot (plot) and sex. Regression coefficients (β) are presented with standard error (SE), z-statistic (z), and P-values (P). * = significant at $P < 0.05$, ** = significant at $P < 0.01$, *** = significant at $P < 0.001$.

Model type	Variable	β	SE	z	P
Count model	Intercept	1.63	0.10	16.42	<0.001***
	Plot				
	1.5	-0.13	0.12	-1.05	0.29
	3	-0.59	0.21	-2.79	<0.01**
	5	-1.40	0.47	-3.01	<0.01**
	Sex				
	Male	0.06	0.11		0.59
Zero-inflated model	Intercept	-0.83	0.41	-2.01	<0.05*
	Plot				
	1.5	0.19	0.53	0.37	0.71
	3	2.20	0.53	4.13	<0.001***
	5	2.74	0.69	3.95	<0.001***
	Sex				
	Male	-0.64	0.40	-1.58	0.13

(range = 245–3,589) after release. Just over half (53.52%, 15/28) of tortoises surviving the length of the study reused a location they established in summer of 2008.

Site fidelity, settlement areas, and home ranges

Desert tortoises on plots 1.5 and 8 showed higher site fidelity and were less likely to reject their release plots than tortoises on plots 3 and 5. Overall, 102 tortoises (64.6%, 102/158) survived past the first year. The last locations of 52.9% of these surviving tortoises (54/102) were within 1.6 km of where they were released. Thirty-one of these were never located outside of these areas, primarily on plots 1.5 ($n = 12$) and 8 ($n = 9$) compared to plots 5 ($n = 6$) and 3 ($n = 4$); 8 of these tortoises survived until the end of the study: 6 (5 females, 1 male) on plot 8 and 2 males on plot 1.5. Desert tortoises located outside the settlement area ($n = 71$) took a mean of 280.1 ± 807.6 days (range = 4–3,684 days) to move beyond it.

Sizes of settlement areas varied among plots and between sexes, with no interaction between the 2 variables (2-way ANOVA; plot, $F_{3,98} = 3.407$, $P = 0.021$; sex, $F_{1,98} = 1.669$, $P = 0.001$; Table 6). Tortoises released on plot 3 had larger radii of settlement areas compared to tortoises released on plots 1.5 and 8 (Tukey's *post hoc*, $P = 0.040$). As might be expected, the radii of settlement areas used by males was larger than females (Tukey's *post hoc*, $P = 0.001$). Overall, the radii of settlement areas averaged 1.95 ± 1.52 km and were larger than our initial estimations. Female tortoises on plot 8 had both the smallest (0.25 km) and largest (8.17 km) radii.

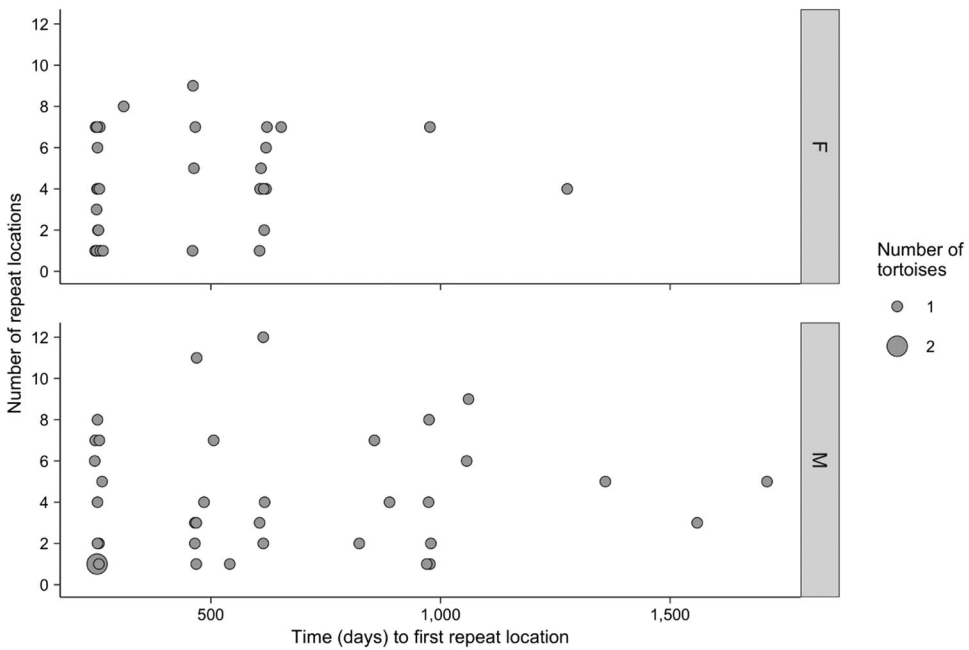


FIGURE 4 Number of repeat locations by sex, and the time required for an Agassiz's desert tortoise to establish its first repeat location during periods of temperature extremes after translocation from the National Training Center, Fort Irwin, in the central Mojave Desert, California, USA, between summer 2008 and summer 2018. Females (F) are in the top part of the figure and males (M) are in the lower part of the figure.

Sizes of use areas varied among plots and between sexes, with no interaction between the 2 variables (Table 6). As expected, males had larger MCP home ranges and core use areas (2-way ANOVA; MCP: $F_{1,145} = 20.074$, $P < 0.001$; core area: $F_{1,140} = 27.039$, $P < 0.001$). Core use area also differed between plots (2-way ANOVA; $F_{3,140} = 5.854$, $P = 0.001$). Tortoises released on plot 8 had smaller core use areas compared to tortoises released on plot 3 (Tukey's *post hoc*, $P = 0.001$) and 5 (Tukey's *post hoc*, $P = 0.026$), and tortoises released on plot 1.5 had smaller core use areas compared with plot 3 (Tukey's *post hoc*, $P = 0.042$).

Models of survival for the released population

After removing missing tortoises from the analysis, the maximum sample size was 149 individuals (100 alive, 49 dead) in the 2008 model, and the minimum was 131 individuals (27 alive, 104 dead) in 2017 (Table 7). In terms of variable importance, number of repeat locations was 1.00 in the general linear models for each year, with a positive model coefficient, indicating that tortoises with greater site fidelity (i.e., more repeat locations [burrows]) were more likely to survive (Table 7). The logistic regression model indicated that tortoises with 5 repeat burrows had a 50% chance of survival, and chances of survival increased with increasing numbers of repeat burrows (Figure 5). Additional variables with importance values ≥ 0.50 were distance traveled per observation, sex, size, and plot. These variables had importance values ≥ 0.50 in the first 3 years post-translocation and distance traveled and size were also important in later years (Table 7). Model coefficients indicated that tortoises moving large distances between observations, females, and tortoises on plots 1.5, 3, and 5 were less likely to survive.

TABLE 6 Summary of use areas by release plot and sex established by 158 Agassiz's desert tortoises translocated from the Fort Irwin National Training Center, California, USA, from spring 2008 through fall 2018. Use areas included home range = home range measured using minimum convex polygons; core use areas = areas where tortoises spent 50% of time; and settlement area radius = radius of the minimum bounding circle of all observed locations.

Plot	Sex	Number of observations			Home range (km ²)			Core use area (km ²)			Settlement area radius (km)		
		\bar{x}	SD	Range	\bar{x}	SD	Range	\bar{x}	SD	Range	\bar{x}	SD	Range
1.5	Female	67.7	43.4	10–147	1.7	1.6	0.2–6.7	0.8	1.1	0.04–3.7	1.2	0.8	0.5–3.6
	Male	94.4	49.2	21–150	3.2	3.2	0.9–12.6	1.5	1.6	0.09–4.8	1.8	0.9	0.9–4.3
3	Female	35.3	40.1	3–145	3.4	5.0	0.01–18.9	2.3	4.1	0.1–14.6	2.0	1.0	0.4–3.3
	Male	38.3	33.6	2–146	7.5	9.4	<0.01–37.2	5.4	10.4	0.2–44.2	2.8	1.8	1.0–7.9
5	Female	30.2	8.4	8–46	2.0	2.5	0.2–8.6	1.0	1.6	0.06–6.7	1.8	1.0	0.3–3.2
	Male	43.0	29.4	13–141	5.6	5.4	0.8–20.0	4.0	4.9	0.3–18.1	2.3	1.1	0.8–4.0
8	Female	94.2	55.8	1–151	2.0	3.9	0.1–15.8	3.4	13.6	0.03–57.7	1.3	1.9	0.2–8.2
	Male	88.0	50.0	6–149	8.9	13.0	0.6–46.8	4.2	8.8	0.06–37.5	2.6	1.9	0.7–6.8

TABLE 7 Importance values of predictor variables used to explain survival in adult Agassiz’s desert tortoises translocated from Fort Irwin National Training Center, in the central Mojave Desert, California, USA, spring 2008 through fall 2018. Total model set (main effects only) included 16 models in 2008 and 32 models from 2009 through 2018. Distance = mean distance that a tortoise traveled per observation; sex = male or female adult; size = straight-line carapace length at the midline (mm); plot = 4 plots where tortoises were released; repeat L = number of repeatedly used locations (burrows) during periods of temperature extremes (i.e., late fall and winter or in summer). The number of tortoises included in the model (n) did not include missing tortoises because status (live or dead) was unknown.

Variable	Importance values by year										
	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Distance	0.538	0.657	0.262	0.262	0.570	0.351	0.334	0.286	0.292	0.283	0.301
Sex	0.735	0.809	0.586	0.278	0.302	0.367	0.288	0.319	0.333	0.325	0.304
Size	0.865	0.389	0.521	0.397	0.266	0.340	0.407	0.525	0.439	0.446	0.333
Plot	1.000	0.998	0.200	0.171	0.109	0.142	0.093	0.047	0.077	0.069	0.131
Repeat L		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
n	149	144	145	141	141	139	136	134	133	131	132
Live	100	68	59	53	52	43	36	33	31	27	28
Dead	49	76	86	88	89	96	100	101	102	104	104

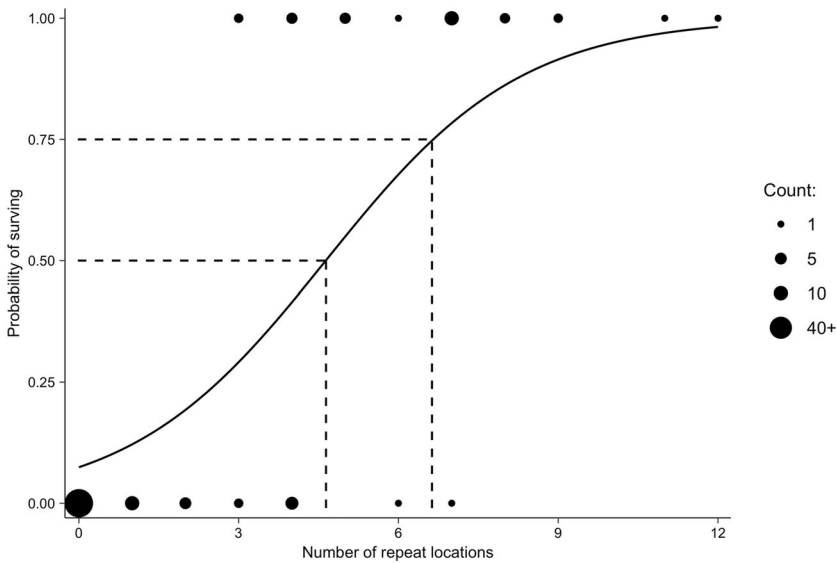


FIGURE 5 Probability of survival after 10.5 years for the 158 adult Agassiz’s desert tortoises translocated from the National Training Center, Fort Irwin in the central Mojave Desert, California, USA, in 2008 to 4 release plots. The driver of survival was the number of repeatedly used locations (burrows) over the course of the study.

In terms of model fit, the number of repeat locations was in the best fit models from 2009 to 2018 (Appendix A, Table A1). From 2011 to 2018, a model with only number of repeat locations was either the best fit model (2011, 2013, 2014, 2018) or performed similarly (i.e., $\Delta AIC_c < 2$) to the best fit model (2015, 2016, 2017), except for 2012 (Appendix A, Table A1). Other variables included in a best fit model were size of the

tortoise (4 models), sex (3 models), average distance between observations (3 models), and release plot (2 models).

DISCUSSION

We predicted that survival would be similar across release plots, but tortoises were most likely to survive on one plot, the plot closest to the original home sites on the NTC. Tortoises released on this plot had greater initial and long-term fidelity to the plot; they traveled shorter distances, dispersed less, particularly during the first year, exhibited smaller settlement areas, and established more repeat locations. As predicted, smaller females were more vulnerable to death, especially early in the study, prior to settling. Females, after settling and establishing repeat locations, which they did faster than males, were no longer more likely to die than males. We also predicted that males would be vulnerable because of traveling longer distances than females. In contrast, males were more likely to survive if they were in the largest adult size class.

Survival

Over the life of the project, few tortoises survived, and most survivors were male. If measured using demographic losses and dispersal of the tortoises during the first 2 years, the release cost was high, especially for a threatened species (Bertolero et al. 2018). Unfortunately, the translocated animals continued to die or be killed until >50% were dead at the end of 2010, the third year. Few remained alive on 3 of the 4 plots after 10.5 years. Measured in terms of a wild population of chelonians, the deaths of >50% of adults over 10 years would be treated as a catastrophe (Keevil et al. 2018, Berry et al. 2020). This and many other species of tortoises and turtles are susceptible to such events because of their life-history traits (Brooks et al. 1991; Congdon et al. 1993, 1994; Garber and Burger 1995). Because 65.2% mortality of wild, translocated adults occurred, we considered this an unsuccessful translocation.

Multiple factors (e.g., size, sex, plot, distances traveled per observation, and numbers of repeatedly used locations) influenced survival. These factors varied in importance depending on the year or years post release and were often inter-related. Although not included in our models, subsidized predators (coyotes, ravens) and other carnivores were drivers of extraordinarily high mortality at least during the first 2 years of the project and played an important role in subsequent years. Subsidized predators were supported by anthropogenic sources of food and housing within and adjacent to the study area (Esque et al. 2010). Also, during 2008 and 2009, mortality was high in tortoises elsewhere in parts of the Mojave Desert (Esque et al. 2010, Cypher et al. 2018), in part because of drought during 2007, the year before translocation. Using modeling, Esque et al. (2010) reported that size of the human population, surface roughness, size and sex of the tortoises, elevation, and road density contributed to the likelihood of deaths from predators in the translocation area. The authors concluded that translocation did not contribute to mortality using the variables included in their models. The interpretations of Esque et al. (2010) are counter to our findings, and we offer 3 explanations for the differences. First, a sample of tortoises was not left on original home sites on the NTC as a control. Instead, both controls and residents for the translocation plots described in Esque et al. (2010) were within the greater translocation area where plots were placed. Second, the plot closest to the original homesites on the NTC experienced lower mortality during the first 2 years of the study and throughout the 10.5-year project, indicating differences in vulnerability to death. Third, translocated individuals were placed in areas where resident tortoises lived. As reported with other species of tortoises, survival is lower when translocated animals are placed where previously released tortoises or resident tortoises live (Tuberville et al. 2008, Bertolero et al. 2018, Pille et al. 2018).

Survival rates for wild adult desert tortoises in non-translocated populations varied from 0.83 to 0.997 in the past with location and drought conditions at sites throughout the geographic range (Turner et al. 1987, Longshore et al. 2003,

Agha et al. 2015). In a 5-year study of a short-distance translocation (≤ 500 m) of wild tortoises (Farnsworth et al. 2015), Dickson et al. (2019) assessed probability of annual survival at >0.87 for large immature and adult tortoises with no significant differences between control, resident, and translocated tortoises. Four studies documented survival among translocated desert tortoises previously held captive as pets or removed from areas under development to the Desert Tortoise Conservation Center in Nevada; survival rates ranged from estimates of 60% to 100% for adults or mixes of adults and immature tortoises over periods of 1–3 years (Field et al. 2003, 2007; Nussear et al. 2012; Scott et al. 2020; L. Allison, USFWS, unpublished data).

Studies of other species of translocated adult testudinids from a variety of sources revealed a range of responses to translocation. Five out of 7 captive Egyptian tortoises (*Testudo kleinmanni*), an endangered, small desert species, translocated to a protected area in Egypt survived (Attum and Rabia 2016). Translocated tortoises living in more mesic environments with higher rainfall, less extreme temperatures, and habitats with higher cover of shrubs, trees, and grasses showed greater short- and long-term survival than we observed (Bertolero et al. 2007, 2018; Tuberville et al. 2008; Pille et al. 2018). Authors generally reported lower survival in the first year following release and lower survival in the second and subsequent releases at the same translocation site for captive gopher tortoises (*Gopherus polyphemus*) and Hermann's tortoise (*Testudo hermannii*) released to protected areas in the southeastern United States and Spain, respectively (Bertolero et al. 2007, 2018; Tuberville et al. 2008). When translocated captive tortoises were released to sites with residents, survival was generally lower for the translocated tortoises (e.g., gopher and Hermann's tortoises; Bertolero et al. 2018, Pille et al. 2018). Some gopher tortoises translocated to a protected area because of development died of stress-related starvation within the first 2 years; models indicated that deaths occurred at sites with higher densities of translocated tortoises (Cozad et al. 2020). Long-term analyses of survival of translocated captive gopher and Hermann's tortoises in protected areas was high: ≥ 0.90 annually for subadult and adult gopher after approximately 12 years (McKee et al. 2021) and 0.978 after 14 years and 0.972 after 29 years for Hermann's tortoises (Bertolero et al. 2007, 2018). Predators negatively affected success of translocations of gopher and Herman's tortoises (Ashton and Burke 2007, Bertolero et al. 2007, Pille et al. 2018). Ashton and Burke (2007) predicted that a specific re-located gopher tortoise population would not remain viable without predator control, and Bertolero et al. (2007:366) reported that "...predators (even at very low densities) can jeopardize a reintroduction" and that they significantly decreased survival of translocated tortoises. Pille et al. (2018) also described deaths from carnivorous predators but did not recommend control.

Choice of plots and study area: potential effects on survival

In the initial planning and selection of potential release plots, Heaton et al. (2008) assumed that the selected plots were sufficiently similar in habitat and other variables to original home sites and that tortoises would accept and stay on release plots (Stamps and Swaisgood 2007, Berger-Tal et al. 2020). Some tortoises rejected the plots and dispersed, and some died after dispersal. We do not know the factors that the tortoises used in accepting or rejecting the plots in this or any study of desert tortoise translocation.

We suggest that the translocated tortoises on the 4 plots created localized source-sink dynamics (Pulliam 1988, Loreau et al. 2013, Bauder et al. 2014, Zipkin and Saunders 2018). Source-sinks may have contributed to high mortality and concomitantly low survival throughout the study. We base these retrospective observations on a review of the translocation area and plots selected by Heaton et al. (2008). In 2004–2005, prior to translocation, the USFWS (2015) estimated densities of resident adult tortoises at 6.4 adults/km² for the Superior-Cronese critical habitat unit where the translocation later occurred. In contrast, densities of adults on release plots at the time of release were approximately 40 adults/plot or 15.5 adults/km², >2 times that of the surrounding resident population. Several decades ago, habitat may have supported ≥ 15 adult tortoises/km² in the region (USFWS 1994, Berry and Murphy 2019). Declines in abundance occurred prior to, during, and after the release; the USFWS (2015) reported a 61.5% decline in adult tortoises in the Superior-Cronese critical habitat unit between 2004 and 2014 to

2.4 adults/km², despite additions of several hundred tortoises from the NTC translocation project in 2008. By 2017, the density of adults had declined further to 1.7 adults/km² (USFWS 2018).

The condition of habitat on and in the vicinity of plots was an additional assumption. Multiple anthropogenic activities contributed to degraded habitat and probably to loss of tortoises (Berry and Murphy 2019). Habitat in the translocation area was degraded and fragmented by a history of livestock grazing, mining, military uses, transmission line and utility corridors, roads, and vehicle trails and tracks from recreational use (USBLM 1980, 2019; Berry and Murphy 2019; Figure 1) These disturbances were sources of the elevated biomass of invasive, non-native annual plants that competed with native forbs used by the tortoise for forage (Brooks 2000, Brooks and Berry 2006, Jennings and Berry 2015). More than 60% of the biomass was composed of non-native species in wet years and >90% in dry years, limiting food choices for tortoises (Brooks and Berry 2006). In addition, parts of the translocation area associated with the plots were barren or almost barren of shrubs (Figure 1; Coyote Dry Lake, the Manix Trail for military tank traffic, and former start area and route of the Barstow to Las Vegas motorcycle race). Populations of resident tortoises were also depleted adjacent to the interstate highway (I-15) and Fort Irwin Road (Figure 1) from vehicle kills and illegal collections, a pattern observed elsewhere in association with roads (von Seckendorff Hoff and Marlow 2002, Nafus et al. 2013).

Dispersal, retention, and settlement

Dispersal affects success of a translocation positively if tortoises remain and survive on site and potentially negatively if they leave, travel until energy reserves are exhausted, experience hyper- or hypothermia, cross hostile terrain, settle in inappropriate areas, or enter an area with higher probability of death. Retention and settlement on site can be important management objectives for measuring success. In general, translocated testudinids may disperse from release sites, attempt to return home, or find a place like home at or near the release site (Berry 1986a, Seigel and Dodd 2000, Stamps and Swaisgood 2007, Tuberville et al. 2008, Nussear et al. 2012). According to the natal habitat preference induction theory, dispersal can be treated as a rejection of the release site (i.e., a forced dispersal) because key elements comparable to the original home site are missing (Stamps and Swaisgood 2007). Thus, comparable habitat between home and release sites is essential for retention on site, as is identifying and understanding critical and important elements for each species (Stamps and Swaisgood 2007). Tortoises in a long-distance translocation moved to release sites in atypical habitats, described by Nussear et al. (2012), were still dispersing at the end of the third year of tracking. Dispersal patterns of desert tortoises in our study were comparable to those of other desert tortoises in long-distance translocations or homing experiments (Berry 1986a, Field et al. 2007, Nussear et al. 2012, Hinderle et al. 2015). The exception was the greater lengths of dispersals we documented.

Season of release and whether a release is soft or hard may affect the extent of dispersal, survival, retention, and settlement in testudinids (Field et al. 2003, Tuberville et al. 2005, Attum and Rabia 2016, Pille et al. 2018). The hard release in our study allowed tortoises approximately 4–6 weeks to settle and find a burrow before ground and air temperatures exceeded the critical thermal maximum for body temperatures (Brattstrom 1961, 1965). In contrast, a release prior to dormancy in early October could force construction of a burrow or shelter within 2–3 weeks and potential settlement before onset of freezing temperatures. For gopher tortoises, penning prior to release resulted in a higher percentage of retention at the release site compared to non-penned individuals (Tuberville et al. 2005). Hard releases resulted in greater dispersal in some testudinids compared to soft releases, but the results were not consistent (Tuberville et al. 2005, Attum et al. 2007, Pille et al. 2018).

Bertolero et al. (2018) emphasized the importance of long-term survival of long-lived tortoises for establishing and maintaining a viable population, and Seigel and Dodd (2000) concluded that annual retention rates of $\geq 90\%$ would be necessary to maintain a viable population of long-lived turtles. We did not meet either objective. In our study, retention on or closely associated with the plots was low overall but higher for the plot closest to original

home sites, providing potential clues for future study. Selection of sites that enhance retention, reduce dispersal, and increase survival are among important topics for future research on translocation of desert tortoises.

MANAGEMENT IMPLICATIONS

Future challenges for the translocation of desert tortoises will involve finding suitable habitat with adequate native forage and minimal anthropogenic effects. If such areas are unavailable, then unacceptably low survival rates of released tortoises may become an important consideration prohibiting such projects and requiring the development of alternative conservation strategies. Success of future translocation projects, measured in terms of survival and dispersal of released tortoises over 20–30 years, is likely to depend on in-depth evaluations of original home sites and comparisons with potential release areas. In-depth evaluations include cover and diversity of native perennial shrubs, trees, bunch grasses, and biomass of annual plants by species. The proportion of annual biomass in non-native species is crucial to the evaluation. Knowledge of the presence, distribution, and abundance of potential predators is essential to survival and long-term viability of translocated tortoises. Future planning for translocations would benefit from multi-year field evaluations of presence, abundance, and distribution of subsidized and other predators. Release sites highly fragmented by dirt and paved roads, routes, trails, campsites, and shooting areas are unlikely to support viable populations. Protection of selected release sites from vehicles, livestock, feral ungulates, and other related human activities, potentially by fencing or designation as a reserve, could be beneficial for increasing survival and forming viable tortoise populations.

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CONFLICTS OF INTEREST

The authors have no conflicts of interest.

ETHICS STATEMENT

We received permits for all activities described herein prior to release and during 2008 under USFWS Recovery Permit TE-102235-1, -2, -3, and California Department of Fish and Game Memorandum of Understanding 801179-01, permanent SC-002235. From 2009 through 2018, we tracked and handled translocated tortoises under Federal permits TE-102235-2, -3, -4, -05; CDFG SC 011076; TE-06556-16, -17 and California Department of Fish and Wildlife SC-003623, SCP801063-04; USFWS TE 87850-0, TE 98950B-0; TE-32004C-2 and California Endangered Species Act Memorandum of Understanding 2081a-2017-001-R6.

DATA AVAILABILITY STATEMENT

Data are part of a larger project and probably will become a USGS Data Release after project completion.

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APPENDIX A: MODELS ESTIMATING VARIABLES AFFECTING SURVIVAL OF ADULT AGASSIZ'S DESERT TORTOISES TRANSLOCATED FROM FORT IRWIN NATIONAL TRAINING CENTER, CALIFORNIA, USA.

TABLE A1 Models for evaluating behavioral variables associated with survival of translocated Agassiz's desert tortoise from the National Training Center, Fort Irwin, California, USA, 2008–2018. We measured performance of generalized linear models ranked according to corrected Akaike's Information Criterion (AIC_c), difference in AIC_c relative to the best model (ΔAIC_c), Akaike weight, cumulative weight, and evidence ratios. Plot = 1 of 4 plots where tortoises were released, sex = male or female, MCL = carapace length at the midline of tortoises, dist = average distance that a tortoise traveled per observation; repeat L = number of locations or repeatedly used locations (burrows) for times of extreme temperatures (late fall, winter, summer). Surviving tortoises settled early, repeatedly using locations where they constructed burrows, compared with tortoises that died or disappeared, although plot location (closer to home sites), larger size, and sex (males) contributed to survival, especially during early years.

Year	Model	AIC_c	ΔAIC_c	Akaike weight	Cumulative weight	Evidence ratio
2008	Plot, sex, MCL, dist		0.000			
2009	Plot, sex, dist, repeat L	141.2	0.000	0.47	0.47	1.00
	Plot, sex, MCL, dist, repeat L	142.7	1.532	0.22	0.69	2.15
2010	Sex, repeat L	94.8	0.000	0.19	0.19	1.00
	MCL, repeat L	95.9	1.145	0.11	0.30	1.77
	Plot, MCL, repeat L	96.1	1.254	0.10	0.40	1.87
	Sex, dist, repeat L	96.1	1.259	0.10	0.50	1.88

TABLE A1 (Continued)

Year	Model	AIC _c	ΔAIC _c	Akaike weight	Cumulative weight	Evidence ratio
2011	Sex, MCL, repeat L	96.1	1.264	0.10	0.60	1.88
	Plot, sex, repeat L	96.4	1.590	0.09	0.69	2.21
	Plot, sex, MCL, repeat L	96.8	1.966	0.07	0.76	2.67
	Repeat L	66.6	0.000	0.27	0.27	1.00
	MCL, repeat L	67.6	1.014	0.17	0.44	1.66
	Sex, repeat L	68.5	1.931	0.10	0.54	2.63
	Dist, repeat L	68.6	1.987	0.10	0.64	2.70
2012	Dist, repeat L	36.3	0.000	0.39	0.39	1.00
2013	Repeat L	59.8	0.000	0.19	0.19	1.00
	Sex, dist, repeat L	60.2	0.400	0.15	0.34	1.22
	Sex, repeat L	60.3	0.451	0.14	0.49	1.25
	MCL, repeat L	60.5	0.672	0.13	0.62	1.40
	MCL, dist, repeat L	61.2	1.354	0.10	0.72	1.97
2014	Dist, repeat L	61.5	1.652	0.08	0.80	2.28
	Repeat L	58.5	0.000	0.24	0.24	1.00
	MCL, repeat L	58.9	0.410	0.19	0.43	1.23
	MCL, dist, repeat L	60.0	1.477	0.12	0.55	2.09
	Sex, repeat L	60.1	1.614	0.10	0.65	2.24
2015	Dist, repeat L	60.3	1.840	0.10	0.75	2.51
	MCL, repeat L	46.4	0.000	0.28	0.28	1.00
	Repeat L	47.4	1.004	0.17	0.45	1.65
	MCL, dist, repeat L	48.1	1.698	0.12	0.57	2.34
	Sex, repeat L	48.2	1.837	0.11	0.68	2.50
2016	Sex, MCL, repeat L	48.3	1.919	0.12	0.80	2.61
	MCL, repeat L	40.0	0.000	0.23	0.23	1.00
	Repeat L	40.3	0.296	0.20	0.43	1.16
	Sex, repeat L	40.9	0.860	0.15	0.58	1.54
2017	MCL, dist, repeat L	41.7	1.663	0.10	0.68	2.30
	MCL, repeat L	50.0	0.000	0.23	0.23	1.00
	Repeat L	50.1	0.125	0.21	0.44	1.06
	Sex, repeat L	50.9	0.943	0.14	0.58	1.60
2018	MCL, dist, repeat L	51.7	1.737	0.09	0.67	2.38
	Repeat L	46.9	0.000	0.24	0.24	1.00
	MCL, repeat L	47.7	0.808	0.17	0.41	1.50
	Sex, repeat L	47.8	1.090	0.14	0.55	1.72
	Dist, repeat L	48.3	1.538	0.12	0.67	2.05